A QUANTITATIVE ANALYSIS OF PLANT GROWTH.

PART I.

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(With 9 text-figures.)

Introduction.

The quantitative analysis of plant growth is a branch of plant physiology to which adequate attention has not as yet been paid, but which should be able nevertheless to yield results of much theoretical interest and economic importance. Methods for obtaining data for the analysis of plant growth under ordinary cultural conditions are in general simple, consisting principally of periodic dry-weight and leaf-area measurements, and a quantity of excellent data of this nature has already been collected and exists in the literature. As yet a thorough analysis of these results has not been presented. Attempts have been made to fit in a few isolated results with various empirical laws without wide examination of existing data.

For example it has been recently suggested by V. H. Blackman (1) that the growth of an annual plant can be treated as a process following the compound interest law expressed by the formula

$$W = W_0 e^{rt},$$

where W = the dry-weight of the plant at time t, W_0 = the initial dry weight of the plant, r = the rate of interest or "efficiency index" of dry-weight production, and e = the base of the natural logarithms.

Another suggestion is that the growth of a plant is similar to an autocatalytic reaction, and that it can be expressed by the formula

$$\log \frac{x}{A - x} = K(t - t_1),$$

where A = the maximum dry-weight of the plant, x = the dry-weight of the plant at any time t, t_1 = the time at which the weight of the plant is half the final dry-weight, and K = a constant. This suggestion was put forward by Robertson (24 and 25) and has received the support of Reed and Holland (21) and of Rippel (22 and 23).

Finally Mitscherlich (14, 15 and 16) has attempted to apply to plant growth as measured by dry-weight increase the following formula

$$\log(\sqrt[n]{A} - \sqrt[n]{y}) = \log \sqrt[n]{A} - c \, . \, x.$$

In this formula n = a variable quantity indicating the probable number of environmental factors, A = the maximum possible dry-weight attainable by the plant in question, y = the dry-weight of the plant at time x, the time x being expressed in vegetation periods (Vegetationsabschnitten) of arbitrary length.

A fuller consideration and criticism of these suggestions will be given in subsequent chapters.

In the present paper the primary objective is to attempt to obtain a concrete idea of the growth and development of the plant. At the outset it will be best to confine our attention to simple cases and we propose to devote the first chapter to a consideration of an annual plant.

Certain data are required: periodic dry-weight measurements of the whole plant (and its various parts) at short intervals throughout its life, starting from the seed at the time of sowing; corresponding periodic leaf-area measurements; data with regard to light, temperature, and water supply. To avoid the error due to individual variation, a large number of plants should be used for each dry-weight measurement and where possible uniform 'pure-line' material should be employed.

There are various methods of presenting the results, and in the first instance we shall use the *relative growth-rate curve.* The principle of the proposed method of expressing rate of growth is analogous to that of the method by which the rate of most reactions, both chemical and physiological, are expressed, namely, amount of change per unit of material per unit of time. Since the amount of material in the growing plant is constantly changing, and since the relative rate of growth is not constant, as the following analysis will show, to achieve mathematical accuracy the increase should be measured over an infinitely short period. This procedure is manifestly impossible, and as we have no exact knowledge of the way in which the relative rate of growth varies over a given period we have adopted the following purely conventional method of defining relative rate of growth. The relative rate of growth of a plant during any given week in its life-cycle is the amount

Relative growth-rate curves for "Badischer Früh" Maize, 1876

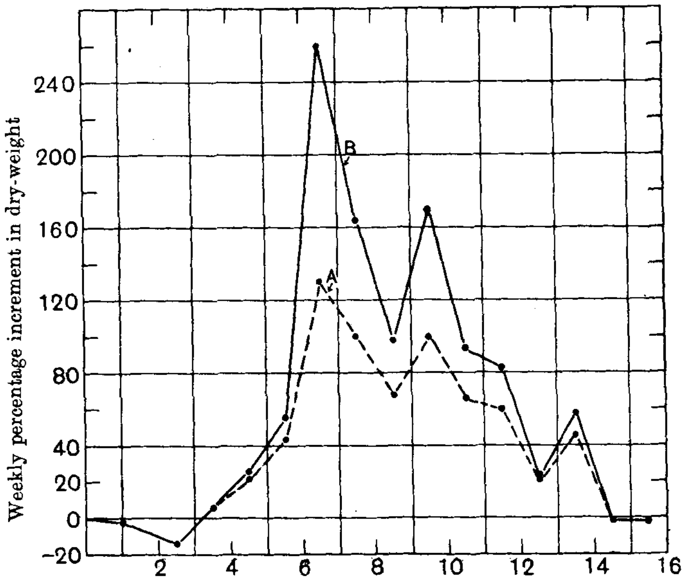


Fig. 1.

of dry matter which 100 g. of dry matter taken at the beginning of the week adds during the week. A week has been chosen since this is the usual interval between determinations of dry-weight in most experiments on growth in plants[1]. It must be realised that the method does not pretend to mathematical accuracy being merely an approximate average for the week, but with such results as are at present available nothing more accurate can be obtained. Even if measurements over

[1] When results are not given for a week we have calculated the increase per 100 g. for the period and divided the result by the number of weeks in the period: for example, if the period is 8 days and 40 g. increases by 20 g. during that period, then the relative rate is $\frac{20 \times 100}{40} \div \frac{8}{7}$.

shorter intervals were available, until we gain knowledge of a mathematical law according to which the rate changes, we cannot determine the rate at any given time.

It might be suggested that allowance could easily be made for the continuous increase in the dry-weight during the week by assuming that this takes place at a uniform rate, and consequently that by means of the following logarithmic formula the rate could be determined:

$$\log W - \log W_0 = r,$$

where $W =$ the dry-weight at the end of the week, and $W_0 =$ the dry-weight at the beginning of the week.

In curve A, Fig. 1, this allowance has been made. In Curve B the ordinates are relative growth-rates calculated by our method, that is, without making allowance for the continuous increase during the week. These curves show similar variations in relative rate from week to week. The more complicated method, however, does not achieve accuracy as it rests on the assumption that the rate remains constant during the week, an assumption manifestly incorrect since the rate varies from week to week. Both methods are purely conventional and only approximate to accuracy, and nothing definite is to be gained by adopting the more complicated procedure.

The relative rate of plant growth at any time may be taken as an expression of the efficiency of the plant at that time in producing dry matter. It must be remembered from what we have said above that the actual value of the figures for the growth-rate is only an average of the changing rate during a week. They are, however, valid for purposes of comparing the rate of a plant's growth from week to week.

The gist of the method described above of presenting the results of growth experiments has been previously briefly put forward by Kidd and West (9).

CHAPTER I.

THE RELATIVE GROWTH-RATE CURVE FOR MAIZE.

The most complete set of data for one plant is to be found in a series of papers published in Germany many years ago under the general direction of U. Kreusler (10, 11, and 13). From among the many results recorded, we have chosen those for maize, since the growth of this plant was studied in four successive years. The data include not only weekly dry-weight measurements and corresponding leaf-area measurements, but also environmental conditions such as light, temperature, water-supply, etc. The dates of the first appearance of the flowers and of seed formation are also given. The work appears to have been carried out without any pre-conceived idea as to what the results would be, and the results themselves have not as yet been worked out nor have they received critical consideration although collected and published 40 years ago. These results will be analysed in this and in the following chapter, and certain interesting conclusions reached. We have constructed from Kreusler's data the tables and figures presented in this paper. Figs. 2 and 3 show respectively the relative growth-rate curves for "Badischer Früh" maize, the rates being calculated, as above described, on the basis of weekly periods for the years 1875–1878 inclusive, and for five different varieties of maize calculated on the same basis for the year 1875.

Table I.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·206						
				(30)*				
1st June	21	0·268	0·062	10	33·3	124	14	
8th "	7	0·559	0·291	108	97·8	177	19·3	
15th "	7	1·069	0·510	91	181·1	170	17·1	
				(129)				
23rd "	8	2·448	1·379	113	405·1	167	16·6	
30th "	7	4·776	2·328	95	889	186	17·0	
7th July	7	11·077	6·301	132	1543	139	19·9	♂ flowers
				(113)				
13th "	6	23·619	12·542	132	2646	112	18·1	♀ flowers
				(85)				
21st "	8	43·844	20·225	74	3633	83	18·8	
				(28)				
27th "	6	55·934	12·090	33	3291	59	17·6	
3rd Aug.	7	72·875	16·941	30	3617	50	16·9	
10th "	7	76·619	3·744	5	3630	48·5	19·1	
17th "	7	84·332	7·713	10	2933	34·5	21·5	
24th "	7	89·621	5·289	6	2696	30	19·8	
31st "	7	100·380	10·759	12	2907	29	19·0	
7th Sept.	7	130·478	30·098	30	2986	23	16·1	
				(21)				
15th "	8	158·139	27·661	18	2335	14·8	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table II.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1876.

Date of harvest 1876	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Number of hours of sunshine	Mean temperature for the week °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·3264							
				(−2·91)*					
24th ,,	13	0·3169	−0·0095	−1·57				9·8	
31st ,,	7	0·2724	−0·0445	−14	8·4	31	42	13	
7th June	7	0·2914	+0·0190	+ 7	19·0	65	61	15·1	
14th ,,	7	0·3642	0·0728	25	41·4	113	16	16·3	
21st ,,	7	0·5674	0·2032	56	92·0	162	57	16·9	
28th ,,	7	2·0733	1·5059	260	350·8	170	102	19	
5th July	7	5·655	3·582	164	987·0	172	42	17·6	
12th ,,	7	11·151	5·496	97	1794·5	159	45	20	
19th ,,	7	30·265	19·114	170	3272·6	108	71	17·6	♂ and ♀
26th ,,	7	58·609	28·344	93	4959·8	85	49	18·5	flowers
2nd Aug.	7	106·908	48·299	83	6196·7	58	93	20·3	
9th ,,	7	131·169	24·261	22·7	5530·7	42	76	18·3	
16th ,,	7	207·373	76·204	58·2	6666·7	32	94	21·9	
23rd ,,	7	204·436	−2·937	−1·42	6201·4	30·5	77	21·6	
30th ,,	7	202·168	−2·268	−1·12	4231·4	21	10	14·5	

* The figure in brackets in column 5 gives the percentage increase in dry-weight for 13 days.

Table III.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1877.

Date of harvest 1877	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Number of hours of sunshine	Mean temperature for the week °C.	Record of appearance of ♂ and ♀ flowers
17th May		0·3353							
				(−3·88)*					
29th ,,	12	0·3223	−0·013	− 1·9			14	11·9	
5th June	7	0·2819	−0·404	−12·6	5·43	19·2	44	16·6	
12th ,,	7	0·2877	+0·0058	+ 2·13	45·7	159	33	19·1	
19th ,,	7	0·9395	0·6518	227	168·8	180	54	18·7	
26th ,,	7	2·500	1·650	176	477·5	192	32	18·8	
3rd July	7	6·365	3·775	150	1060	166	40	18·0	
10th ,,	7	10·637	4·272	67	1671	157	20	14·7	
17th ,,	7	24·447	13·810	130	3216	132	27	19·0	♂ flowers
24th ,,	7	41·408	16·961	69	3788	92	38	17·5	♀ flowers
31st ,,	7	66·498	25·09	61	4591	69	20	18·6	
7th Aug.	7	88·654	22·156	33·4	4934	55·5	40	16·4	
14th ,,	7	119·842	31·188	35	5298	44	19	19·3	
21st ,,	7	135·532	15·690	13	4852	35·5	30	19·5	
28th ,,	7	140·782	5·250	3·9	4158	29·5	17	18·1	
4th Sept.	7	179·973	39·191	28	4332	23	25	16·6	
11th ,,	7	187·795	7·822	4·35	4035	21·5	17	13·0	
18th ,,	7	201·293	13·498	7·2			18	16·0	
25th ,,	7	220·709	19·416	9·4			9	9·7	
2nd Oct.	7	199·970	−20·739	−9·4			22	7·9	
9th ,,	7	204·017	+4·047	+2·0			9	9·0	

* The figure in brackets in column 5 gives the percentage increase in dry-weight for 12 days.

Table IV.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1878.

Date of harvest 1878	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Number of hours of sunshine	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
20th May		0·3282							
28th „	8	0·3280	−0·0002					12·4	
4th June	7	0·2870	−0·041	−12·5			40	13·6	
11th „	7	0·2550	−0·032	−11·2	17·9	70	27	15·5	
18th „	7	0·3080	+0·053	+20·8	29·2	95	19	15·1	
25th „	7	0·6370	0·329	106·5	124·4	195	40	17·9	
2nd July	7	2·319	1·682	264	419·2	181	36	19·8	
9th „	7	4·654	2·335	100	762·2	174	16	17·1	
16th „	7	9·019	4·365	94	1301	144	20	16·8	
23rd „	7	20·001	10·982	122	2136	107	57	19·6	♂ and ♀
30th „	7	34·557	14·556	72	2805	81	23	19·8	flowers
6th Aug.	7	57·587	23·030	66	3384	59	35	18·2	
13th „	7	70·095	12·058	21·7	3047	43·5	32	20·1	
20th „	7	85·165	15·070	21·4	3025	35·5	35	19·3	
27th „	7	111·649	26·484	31	2976	26·5	17	17·8	
3rd Sept.	7	124·760	13·111	11·7	2684	21·5	21	19·0	
10th „	7	121·990	−2·770	−2·2	2387	19·5	35	19·2	

Table V.—"*Hühner*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq.cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·127						
1st June	21	0·149	·022	(17)* 5·7	28·9	194	14·0	
8th „	7	0·476	·327	220	86·3	181	19·3	
15th „	7	0·824	·348	73	153	186	17·1	
23rd „	8	1·765	·941	(114) 100	371	210	16·6	
30th „	7	2·847	1·082	61	627	220	17·0	
7th July	7	7·292	4·445	156	895	123	19·9	♂ and ♀ flowers
13th „	6	11·570	4·278	(59) 69	749	65	18·1	
21st „	8	21·576	10·006	(86) 75	1416	66	18·8	
27th „	6	40·735	19·159	(89) 104	2126	52	17·6	
3rd Aug.	7	55·918	15·183	37	1917	34	16·9	
10th „	7	60·648	4·730	8·5	2196	36	19·1	
17th „	7	73·946	13·298	22	2254	31	21·5	
24th „	7	90·491	16·545	22	2090	23	19·8	
31st „	7	88·212	−2·279	−2·5	2032	23	19·0	
7th Sept.	7	81·618	−6·594	−7·5	1367	17	16·1	
15th „	8	76·385	−5·233	(−6·4) −5·6	665	9	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table VI.—"*Oberländer*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·107						
				(51)*				
1st June	21	0·162	0·055	17	31	192	14·0	
8th ,,	7	0·467	0·304	188	96·7	207	19·3	
15th ,,	7	0·955	0·488	105	165·3	173	17·1	
				(89)				
23rd ,,	8	1·839	0·884	78	374·1	203	16·6	
30th ,,	7	3·097	1·258	67	621·0	201	17·0	
7th July	7	6·758	3·661	118	668·6	99	19·9	♂ and ♀ flowers
				(114)				
13th ,,	6	14·448	7·690	133	950·6	66	18·1	
				(72)				
21st ,,	8	24·890	10·442	63	1098	44	18·8	
				(21)				
27th ,,	6	30·180	5·290	25	1407	47	17·6	
3rd Aug.	7	51·196	21·016	70	1653	32	16·9	
10th ,,	7	70·978	19·782	39	2217	31	19·1	
17th ,,	7	59·110	−11·868	−17	2359	40	21·5	
24th ,,	7	81·687	22·577	38	1464	18	19·8	
31st ,,	7	73·921	−7·766	−9	1235	16	19·0	
7th Sept.	7	74·120	0·199	0·3	1716	10	16·1	
				(18)				
15th ,,	8	87·192	13·072	15	514	6	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table VII.—"*Ungarischer Früh*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·2696						
				(−0·88)*				
1st June	21	0·2672	−0·0024	−0·29	31·0	116	14·0	
8th ,,	7	0·609	0·342	128	118·9	196	19·3	
15th ,,	7	1·110	0·501	82	190·2	172	17·1	
				(93)				
23rd ,,	8	2·143	1·033	81	393·2	184	16·6	
30th ,,	7	4·123	1·980	93	807·0	196	17·0	
7th July	7	12·101	7·978	195	2109	174	19·9	♂ and ♀ flowers
				(92)				
13th ,,	6	23·244	11·143	107	3030	130	18·1	
				(91)				
21st ,,	8	44·48	21·236	80	4329	97	18·8	
27th ,,	6	70·46	25·98	65	5635	80	17·6	
3rd Aug.	7	104·98	34·52	49	8827	58	16·9	
10th ,,	7	92·85	−12·13	−12	4975	54	19·1	
17th ,,	7	121·78	28·93	30	4894	40	21·5	
24th ,,	7	169·53	47·75	38	3454	20	19·8	
31st ,,	7	212·72	43·19	25	4807	23	19·0	
7th Sept.	7	213·29	0·57	0·3	5204	24	16·1	
				(−5)				
15th ,,	8	202·19	−11·10	−4	2738	14	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table VIII.—"*Pferdezahn*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·294						
1st June	21	0·286	−0·010	(−3·4)* −1·1	36·2	126	14·0	
8th "	7	0·517	0·232	80	77·9	150	19·3	
15th "	7	1·023	0·506	98	177	174	17·1	
23rd "	8	1·781	0·758	(74) 65	335	188	16·6	
30th "	7	3·826	2·045	115	730	190	17·0	
7th July	7	9·064	5·238	135	1686	187	19·9	
13th "	6	17·292	8·228	(91) 106	2578	149	18·1	
21st "	8	29·704	12·41	(72) 63	3984	134	18·8	
27th "	6	54·998	25·29	(85) 100	6274	114	17·6	
3rd Aug.	7	73·949	18·95	32	6622	90	16·9	
10th "	7	108·68	34·73	46	8453	77	19·1	♂ and ♀
17th "	7	153·61	45·93	41	8823	57	21·5	flowers
24th "	7	173·18	18·57	12	8258	48	19·8	
31st "	7	210·37	37·19	21	7090	34	19·0	
7th Sept.	7	245·09	34·72	(−16·5) −14·5	9200	38	16·1	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

In forming a clear picture of the growth of the plant as presented by its increase in dry-weight, it is as well to keep in mind the fact that from 80 % to 90 % of the dry-weight is the result of the process known as carbon-assimilation and that the actual percentage of the dry-weight of the plant derived from the mineral constituents of the soil is relatively small (cf. Hornberger(6), Monnier(17), Rabinovitch(20) and others(26, 4, 8 & 3))[1].

[1] Jones and Huston(8) give the following figures for the ash of maize at different periods:

Date of sampling (week from sowing)	Ash (percentage of the total dry-weight of the plant)
3rd	12·0
9th	12·2
11th	8·7
14th	6·0
16th	5·3
18th	4·8
19th	4·1
20th	4·1

Fig. 2. Relative growth-rate curves for five varieties of maize grown at Poppelsdorf in the year 1875.

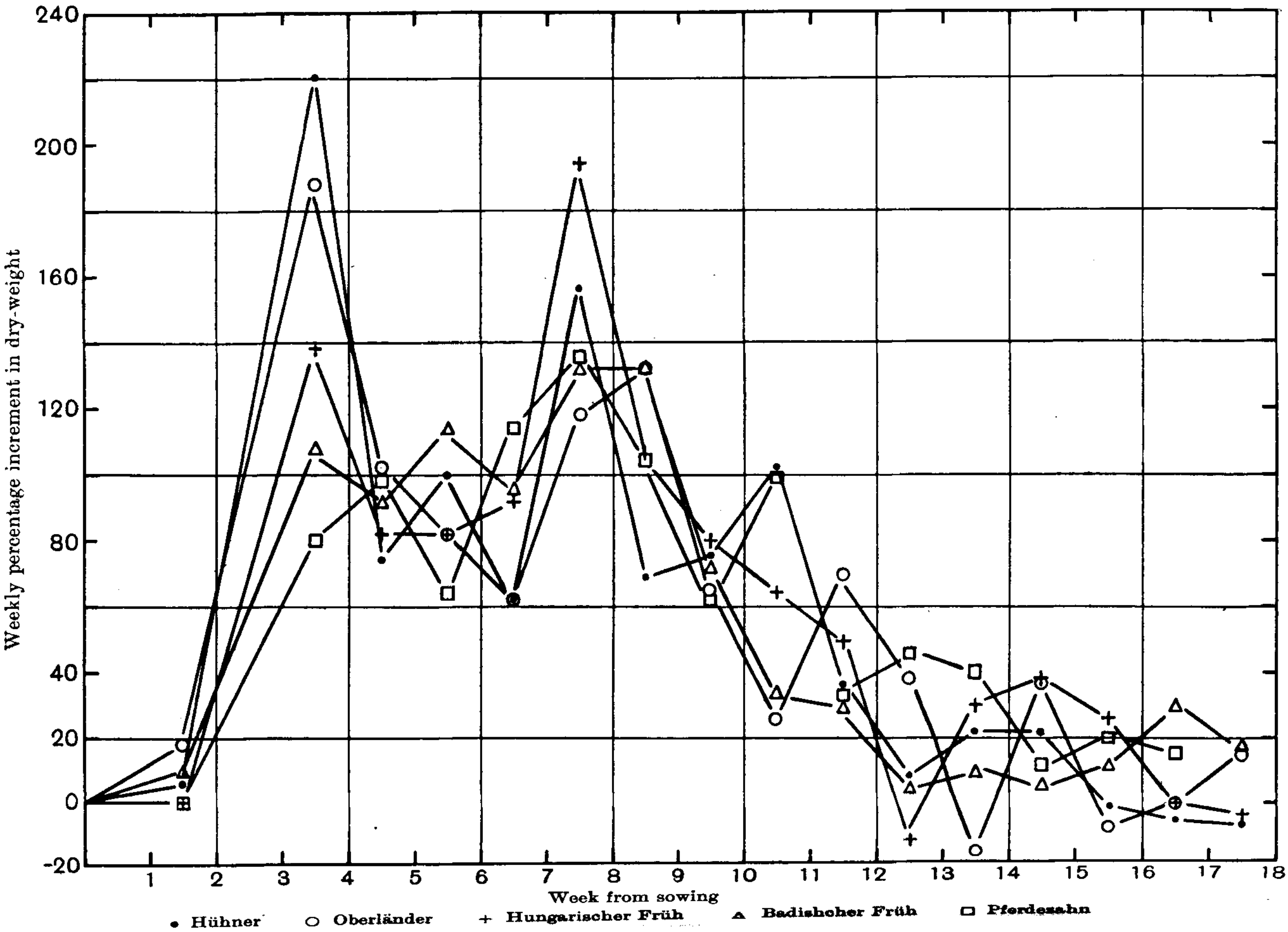
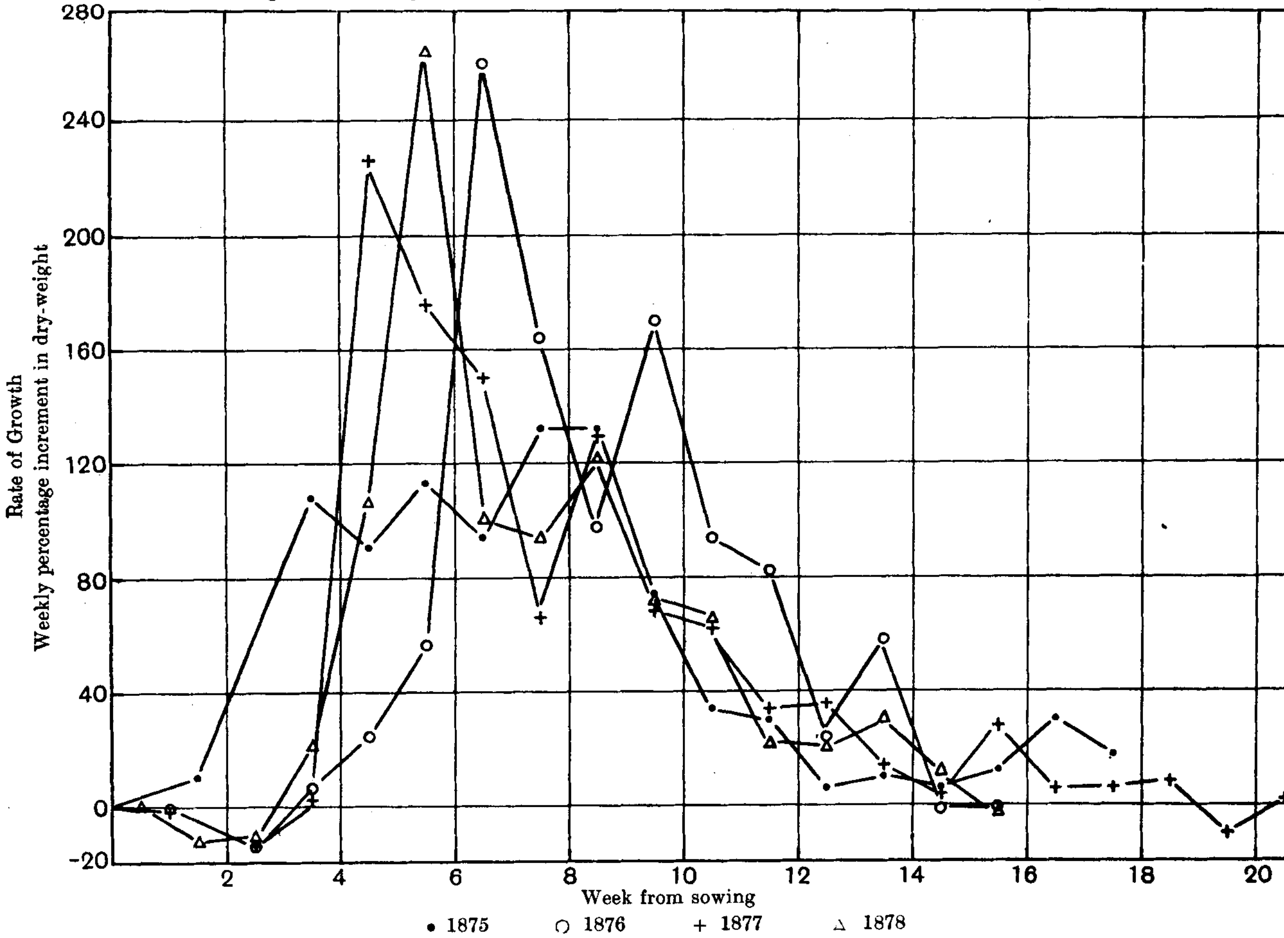


Fig. 3. Relative growth-rate curves for "Badischer Früh" maize in four successive years.



It follows that the relative rate of growth at any time is almost the same as the difference between the rates of assimilation and respiration per 100 g. dry-weight at that time.

We will now proceed to consider the curves. In following the curves in Fig. 3 from the date of sowing, there is seen to be an initial phase lasting for about three weeks during which the rate of growth is negative, in other words, the plant is actually losing in weight[1]. This phase of negative growth persists until a point in the development of the plant is reached at which approximately four leaves have appeared. During the time occupied by germination, before the appearance of these leaves, the negative rate of growth is clearly to be attributed to a loss of carbohydrate through respiration. The order of magnitude of the loss in dry-weight through respiration in germinating seeds is 3 % to 6 % of their dry-weight per day at 16° C. (Garreau (5)). In the latter part of the period, where, despite the fact that the plant possesses from 1–4 leaves, the negative rate of growth persists, it is obvious that any increase in dry-weight due to assimilation is more than counter-balanced by a loss in weight through respiration. Evidence obtained by an analysis of Kreusler's data as to whether the leaves at this stage perform their normal assimilatory function, or not, will be considered shortly. After this initial phase there ensues a short period varying from 1–4 weeks during which the rate of increase in dry-weight rises rapidly to its maximum value, followed by a long period constituting the remainder, and larger part, of the life-cycle of the plant, throughout which the rate of growth falls off more or less continuously. This falling part of the curve, however, shows subsidiary maxima.

The question arises of what kind of change in the plant this perfectly definite type of curve in the main period of growth is an expression. It is clear that this main rise and fall must be due to an increasing difference between the rate of assimilation and the rate of respiration per unit dry-weight in the first phase and to a decreasing difference in the second phase. The order of magnitude of respiration in terms of dry matter consumed per week during the main growth period of the plant is probably not greater than 20 %–40 %, which is the order of magnitude of the loss in dry-weight through respiration during germination. As against this the actual percentage increase in dry-weight per week varies from 0 % to over 200 %, this being the balance when loss due to respiration is

[1] In the year 1875 the first dry-weight measurement was not taken until the end of the third week. The average plotted in Fig. 3 gives no indication of the variations in the individual weekly growth-rates.

subtracted from gain due to assimilation, etc. Consequently it is obvious that changes in the rate of respiration per unit dry-weight of sufficient magnitude to affect the rate of growth to the extent observed are inconceivable. We must turn therefore to the changes in the rate of assimilation per unit dry-weight in order to account for the main rise and fall which characterises the growth-rate curve. Brief consideration will show that the rate of assimilation per unit dry-weight is most probably a function of the amount of leaf-area per unit dry-weight mainly, and it is interesting to enquire therefore to what extent changes in leaf-area per unit dry-weight correspond with those in the rate of growth. The values of the ratio of leaf-area to dry-weight throughout the life-cycle of the plant can be calculated from Kreusler's data, and when these values are plotted against time there appears a striking similarity between this curve and the growth-rate curve (see Figs. 4, 5, 6 and 7).

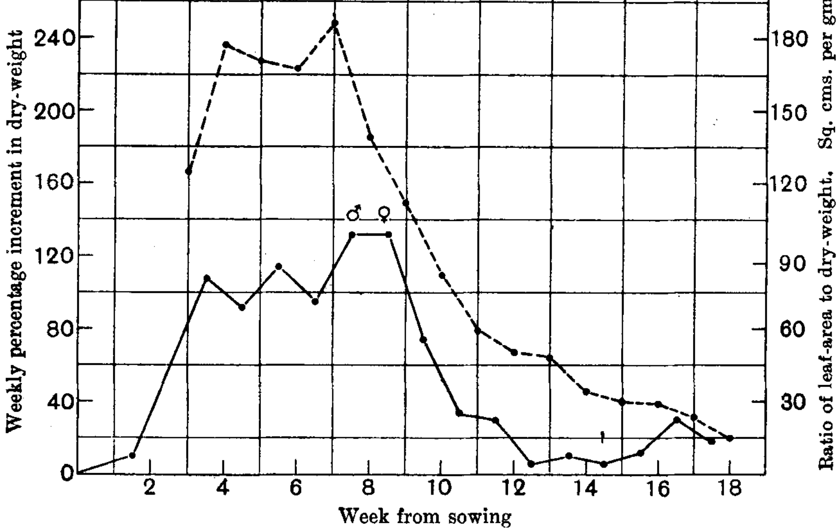
From this we may conclude, therefore, that the main rise and fall shown by the growth-rate curve is merely an expression of the rise and fall in the ratio of leaf-area to dry-weight.

To return to the question of the assimilation of the young leaves on their first appearance, an inspection of Figs. 4, 5, 6 and 7 will show that at this stage the ratio of the ordinate of the growth-rate to that of the leaf-area curve (which ratio is really a measure of the increase in dry-weight *per unit leaf-area*) is a negative or very small quantity compared with the ratio during the main period of high relative rate of growth. This fact strongly suggests that the assimilatory power of the young leaves for some time after their first appearance is negligibly small. It is interesting to find that this inference which is drawn from an analysis of plant growth, as presented in this paper, is corroborated by direct experimentation on the assimilatory power of young leaves (Irving (7) and Briggs (2))[1].

Another point of interest which arises from a comparison of the leaf-area ratio with the growth-rate curve is that, while the growth-rate curve exhibits one or more subsidiary maxima in the falling phase, the leaf-area ratio curve on the other hand falls uninterruptedly.

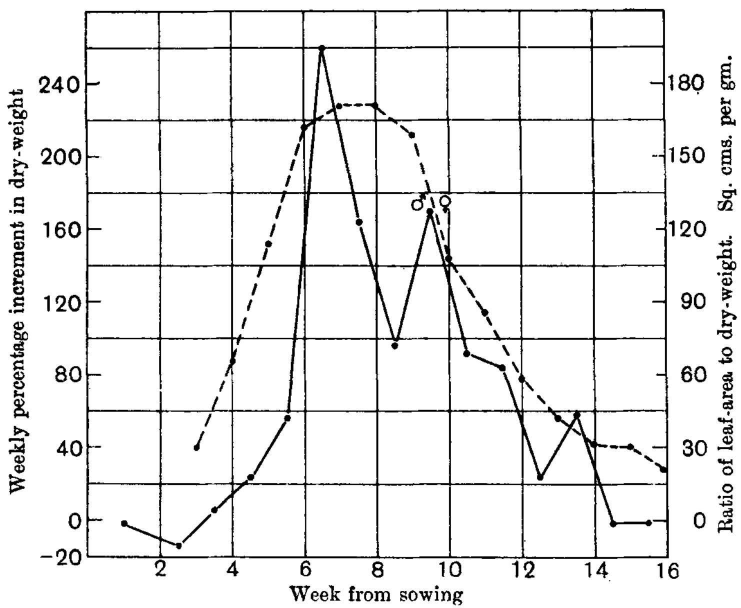
With regard to these subsidiary maxima exhibited by the growth-rate curve there is a significant correlation between the times of their occurrence and the recorded times of the first appearance of the male and female flowers (see Figs. 4–8). Results obtained with maize by Morgen (18) and Osswald (19) who worked in conjunction with Kreusler,

[1] Also unpublished results for maize.



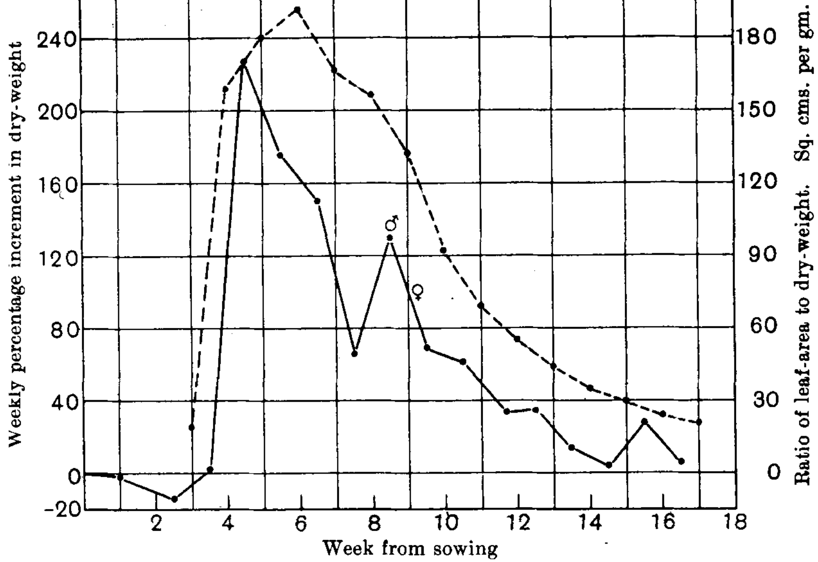
"Badischer Früh" maize 1875 ——— Growth curve ...... Leaf-area ratio curve

Fig. 4.



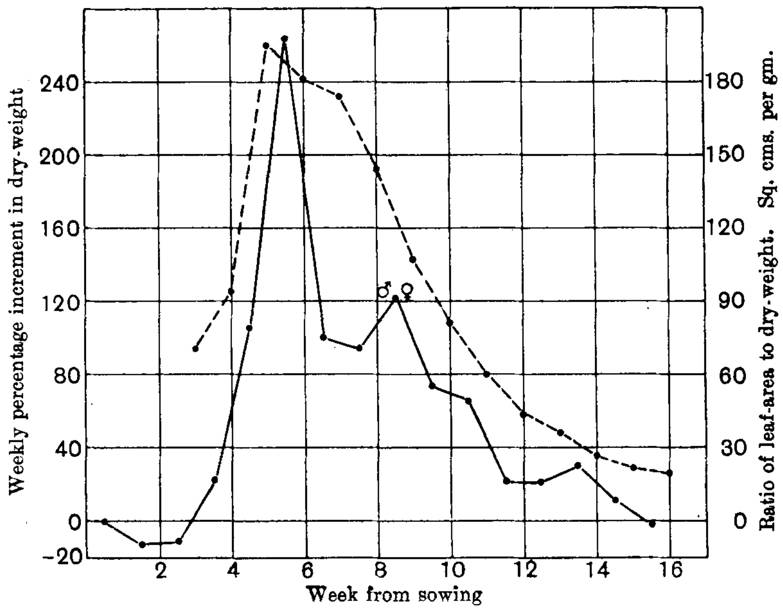
"Badischer Früh" maize 1876 ——— Growth curve ...... Leaf-area ratio curve

Fig. 5.



"Badischer Früh" maize 1877 ——— Growth curve ...... Leaf-area ratio curve

Fig. 6.



Badischer Früh" maize 1878 ——— Growth curve ..... Leaf-area ratio curve

Fig. 7.

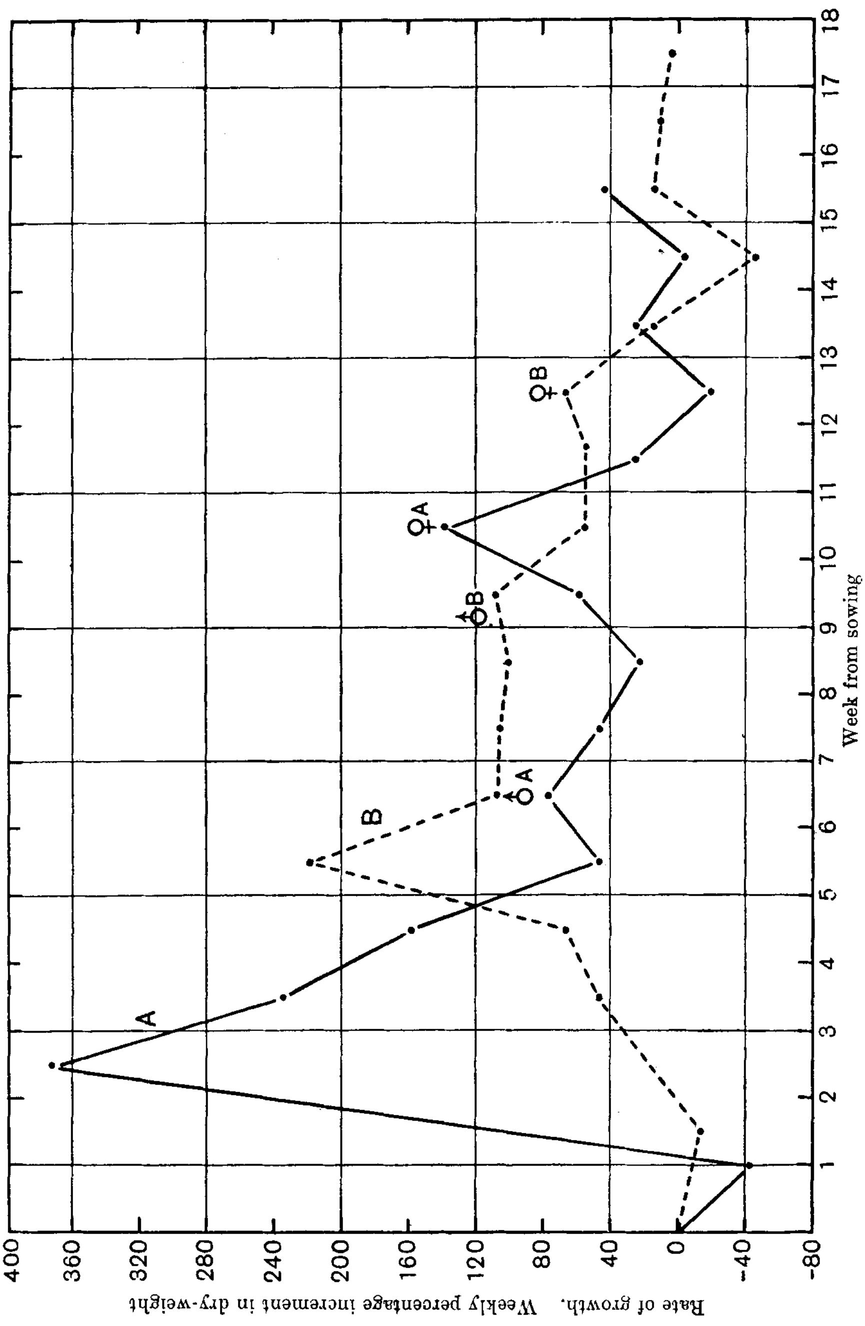
are given in Fig. 8. These results are for tops only, not for the entire plant, including roots, as in the other cases.

It is striking that when there is only one prominent subsidiary maximum the male and female flowers appear together. These subsidiary maxima cannot be correlated with recorded variations in any climatic conditions and consequently it seems safe to conclude that they must be due to internal changes.

In endeavouring to explain these maxima and their correlation with the appearance of the male and female flowers in terms of assimilation and respiration there are two alternatives. The first is to suppose that at the recorded time of the appearance of the flowers there is a temporary increase in assimilation per unit leaf-area or a decrease in respiration per unit dry-weight, or a temporary increase in salt absorption by the roots. The other alternative is to suppose that during the early stages of flower development, prior to the first record, the reverse conditions obtain, in other words, that the minima immediately preceding the record of the appearance of flowers is to be attributed to these reverse conditions. Since it is a well-known fact that flower development is accompanied by an increased respiratory activity and also since we have no evidence that there is an alteration in assimilation per unit leaf-area connected with flower-formation, the safest conclusion at present seems to be that the minima are to be correlated with increased respiratory activity at these periods.

Plants grown at the same time under similar conditions show a coincidence of the maxima (Fig. 2), but when we compare plants grown at different times and under different conditions the incidence of the maxima varies (Fig. 3). It appears likely therefore that the incidence of the maxima depends upon external conditions. As attempts to correlate the maxima with the environmental conditions obtaining at the time of their incidence were unsuccessful, we have concluded that most probably the time of the incidence of the maxima is determined by environmental conditions obtaining at previous stages in the plant's development.

Having now considered the whole of the growth-rate curve for maize it appears on the basis of the data available that the general form of the curve and the occurrence of its various maxima are controlled by internal changes intercorrelated with morphological developments. The points in morphological development which appear to be significant are (1) the rise to a maximum and the subsequent fall in the leaf-area dry-weight ratio, (2) the development of the male flowers, and (3) the development of the female flowers. Environmental conditions may influence



A. "Badischer Früh" maize (Morgen). B. "Italienische Bastard" maize (Osswald). *Tops only.*

Fig. 8.

the time relation of these points and thus the time relations of the maxima on the curve. In extreme cases the environmental factors may so far affect morphological differentiation as to cause coincidence of the maxima.

External conditions, in addition to causing modification in this way in the general form of the growth-rate curve, must directly affect the absolute value of the growth-rate, but an analysis of these curves and attempts to correlate still smaller fluctuations in these curves from year to year with external conditions have not yielded any definite results. We shall return to the subject of the effect of external conditions when dealing later with another form of expressing growth-rate, namely increase in dry-weight per unit leaf-area per unit time.

In a future chapter we propose to compare the relative growth-rate curves of other annual plants with those for maize which have been dealt with above.

Average Growth-Rate.

A full consideration of all the data presented here will show the extraordinary difficulty of finding any valid basis for comparing plants such as maize by means of their average growth-rate whether the average is taken over the whole life-cycle, which is of varying length, or whether arbitrary periods of shorter duration are taken. It is particularly misleading to compare the average growth-rate for one period of one plant with a different period of another plant. For example, a comparison of any two plants by means of their average growth-rate over a period such as six weeks would be favourable to one, whereas a comparison over say 12 weeks might be favourable to the other.

In a subsequent chapter dealing with the question of growth-rate in relation to yield, this point will receive detailed consideration.

Summary.

The series of articles of which this is the first instalment, constitutes an attempt to formulate methods for the quantitative analysis of plant growth and to apply these methods to data which have been lying dormant in the literature for 40 years.

In the present chapter the relative growth-rate curve, which is the weekly percentage increase in dry-weight plotted against time, and also the leaf-area ratio curve, that is, the leaf-area in sq. cms. per g. plotted against time, have been employed. And as a typical example of an

annual plant maize has been selected since data are given by Kreusler for this plant grown in four successive years.

The first noteworthy result of this analysis is the demonstration of the fact that the growth-rate varies greatly in magnitude at different periods in the life-cycle of a plant such as maize in a perfectly definite manner.

Fig. 9 gives the generalised form of the growth-rate curve for maize throughout its life-cycle. Although the broad form is that of a Sach's grand period curve, it must be noted that it is not a grand period curve, since the grand period curve as defined by Sachs is the curve of the actual increment per unit of time plotted against time and not of relative increment, that is, increment per unit of matter per unit of time plotted against time. On the broad form of the relative growth-rate curve

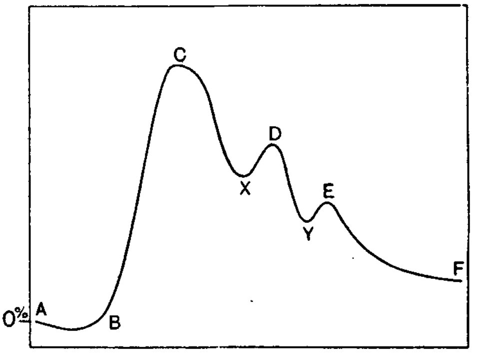


Fig. 9. Generalised form of the growth-rate curve for maize.

for maize are superposed three secondary features, an initial fall, and two subsidiary maxima on the descending limb.

In this generalised curve the initial period A–B is the period before the assimilatory organs are able to counterbalance the loss in dry-weight due to respiration, and the rate of growth is consequently negative or nil. The phase B–C corresponds to a phase in morphological development during which the leaf-area per unit dry-weight increases to a maximum. The phase C–F covers the remainder of the life-cycle of the plant during which the leaf-area per unit dry-weight is continuously decreasing. The subsidiary maxima D and E coincide with the time of the record of the appearance of the male and female flowers respectively. The minima X, Y which precede these maxima, correspond with the earliest stages of flower development, and are possibly due to increased respiration during that period.

The incidence of the maxima is controlled by environmental conditions—not by the environmental conditions operating at the time, but by those obtaining at some previous stage in the life-history of the plant.

The fact that the curve for leaf-area per unit dry-weight throughout the season (which has been calculated) shows a correspondence with the growth-rate curve indicates that the physiological basis for increased and decreased relative rate of growth is a corresponding change in the assimilating area per unit dry-weight. This point will be dealt with in the next chapter.

Evidence from the quantitative analysis of plant growth for maize indicates that the seedling leaves do not perform their normal assimilatory function till some time after their appearance.

(*To be continued.*)

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